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EARLIEST TERTIARY WEST AMERICAN SPECIES OF *PLATYODON* AND *PENITELLA*

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Abstract: Boring bivalve species belonging to the genera *Platyodon* Conrad and *Penitella* Valenciennes are rare in the Cenozoic record of the West Coast of North America. To date, five species, *Platyodon piedraensis* Wiedey, *P. colobus* Woodring, *P. cancellata* (Conrad), *Penitella lorenzana* (Clark), and *P. gabbi* (Tryon) have been recorded from Tertiary formations. Three new species, *Platyodon pecki, P. clarki,* and *Penitella durhami* are described. West American Cenozoic and Recent records of species of the two genera, together with their presently known geographic and temporal ranges, are given. The Japanese Miocene species of *Platyodon, P. nipponica* Uozumi and Fujie, is probably very closely related to *P. piedraensis* Wiedey from the Vaqueros formation of San Luis Obispo region, California.

Introduction

Marine bivalve species belonging to the boring genera *Platyodon* Conrad (Myidae), and *Penitella* Valenciennes (Pholadidae) are rare in both the living and fossil faunas of the West Coast of North America. In all, only three species of *Platyodon* have been recorded, namely *P. piedraensis* Wiedey from the early Miocene, Vaqueros formation of San Luis Obispo County, California, *P. colobus* Woodring from the late Pliocene, San Joaquin formation of the Kettleman Hills area, and *P. cancellatus* (Conrad), undoubtedly known as fossil only from Pliocene and younger strata. The latter occurs today between Bolinas Bay, middle California, and San Diego, southern California (Grant and Gale, 1931, p. 416).

The genus *Penitella* Valenciennes, on the other hand, has a rather restricted geographic distribution. It is known today only from the eastern and northern Pacific (Turner, 1955, p. 71). Only one fossil species, *P. lorenzana* (Clark) has

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been recorded from West American early Tertiary formations (Clark, 1924, p. 107, pl. 18, figs. 5, 6).

According to Turner (1955), at least four species of *Penitella* occur today in the Recent fauna along the eastern Pacific. These are: *Penitella fitchi* Turner, *P. conradi* Valenciennes, *P. gabbi* (Tryon), and *P. penita* (Conrad). At least two of these species, *P. gabbi* (Tryon) and *P. penita* (Conrad), are well known in the fossil record and have been recorded from strata as old as middle Pliocene. Their present geographic ranges as given by Turner (1955) are summarized below: *P. fitchi* is known only from Bahía San Bartolomé (or Bahía Tortuga), Baja California (Turner, 1955, p. 74); *P. conradi* ranges from Gualala, Mendocino County, California south at least as far as Bahía San Bartolomé, Baja California (p. 79); *P. penita* is known from Bering Island, Siberia, south as far as Bahía San Bartolomé (p. 84); and *P. gabbi* ranges from Drier Bay, Alaska, south to San Pedro, California (Turner, 1955, p. 88).

Several well preserved specimens representing three new and most previously described northeastern Pacific Coast species of both *Platyodon* and *Penitella*, are present in the collections of the Museum of Paleontology, University of California, Berkeley (hereafter abbreviated as UCMP). These form the major basis for the present study. One new species of *Platyodon* and one of *Penitella*, namely, *Platyodon pecki* Adegoke, new species, and *Penitella durhami* Adegoke, new species, are described from the basal San Ramon formation (Oligocene) of Contra Costa County, California. Another new species of *Platyodon*, named *P. clarki* Adegoke, new species, is described from the late Miocene San Pablo group of Walnut Creek area, California. The diagnostic features of other previously described northeastern Pacific species of both genera are also briefly reviewed.

Acknowledgments

The author is indebted to Professor J. Wyatt Durham and Mr. J. H. Peck, Jr., of the University of California, Berkeley, for permitting him to study specimens collected by them from the basal San Ramon formation. Mr. Peck also made available for study, type specimens in the Museum collections. Dr. Edwin C. Allison critically read the manuscript and made many helpful suggestions.

Finally, the author thanks his wife, Adekunbi Adegoke, for her assistance in preparing the manuscript.

Stratigraphic Occurrence and Age of New Species

Specimens of the three new species described here were collected from two localities. *Platyodon pecki*, new species, and *Penitella durhami*, new species, were both collected from UCMP locality A-7762 along the contact of the Eocene Alhambra formation (Weaver, 1953, p. 50) with the overlying Oligocene San Ramon formation. *Platyodon clarki*, new species, was obtained from UCMP locality 1942 in the late Miocene San Pablo group.

The unconformable contact of the uppermost Pereira shale member of the Alhambra formation (Weaver, 1953, p. 50) with the overlying San Ramon formation is well exposed near the west end of the second road cut along the Arnold Industrial Highway, about 1¼ miles east of Muir Station, Walnut Creek quadrangle, Contra Costa County, California. In this area, the Pereira shale member is composed of dull gray, greenish- and brownish-gray compact sandy shale and finely bedded silty sandstone containing much muscovite (Weaver, 1953, p. 51), and brown ferruginous stains. The contact of the Alhambra formation with the overlying San Ramon sandstone is disconformable, the latter being deposited on an irregular erosion surface of the former (figs. 23, 26).

The basal San Ramon beds are light brownish- and bluish-gray, medium-grained, micaceous, friable sandstone, with yellow, and brown stains. Sand-filled pelecypod burrows with subrounded cross sections originate in the San Ramon gray sandstones and project half an inch to four inches down into the underlying Alhambra formation (figs. 23, 26). Several specimens of these sand-filled burrows (commonly referred to as "sand-pipes"; see Uozumi and Fujie, 1956; Masuda and Takezawa, 1961; and Itoigawa, 1963) were collected by the writer from this locality. A few of these are figured (figs. 17, 20–23, 25, 26).

The two boring bivalves collected from this locality occur abundantly. These are *Platyodon pecki,* new species, and *Penitella durhami,* new species. All of the well preserved sand-pipes collected belong to *Penitella durhami*, new species.

The fauna and age of the San Ramon formation exposed on both the east and west limbs of the Pacheco syncline were discussed by Arnold (1906, pp. 15–17) and Clark (1918; 1924, pp. 71, 72; 1929, pp. 14–17), and reviewed recently by Weaver (1953, p. 59). This formation was generally assigned an Oligocene age because of its stratigraphic position between strata of late Eocene and early Miocene ages (Weaver *et al.*, 1944, pl. 1), and because many of the species represented in the fauna were similar to those in beds earlier referred to the Oligocene in Washington by Dall (Clark, 1929, p. 15). Clark (1918, pp. 102–105) considered the San Ramon formation to be of middle Oligocene age and compared its fauna to that found stratigraphically between the "*Acila gettysburgensis* zone" and the "*Molopophorus lincolnensis* zone" of Washington. Kleinpell (1938, pp. 56–66, 163) on the basis of foraminiferal faunas assigned the San Ramon formation to his lower Zemorrian (middle Oligocene) Stage.

Platyodon clarki, new species, was first recorded as *Mya (Platyodon) cancellatus* Conrad from UCMP locality 1942 in the San Pablo group by Clark (1915, opp. p. 408). The fossils occurred in coarse-grained, bluish-gray sandstone.

The San Pablo group of Clark (1915) is generally regarded as of late Miocene age (Clark, 1915, pp. 437–442; and Nomland, 1917). These horizons belong to the Cierbo and Neroly "stages" of Weaver and others (1944).

DESCRIPTION OF SPECIES

Phylum MOLLUSCA
Class BIVALVIA
Order Myoida
Suborder Myina
Superfamily Myacea
Family Myidae
Genus **Platyodon** Conrad

Platyodon Conrad, 1837, Jour. Acad. Nat. Sci. Phila., vol. 7, p. 235.
Type species: (monotypic), *Mya* (*Platyodon*) *cancellata* Conrad.

Platyodon pecki Adegoke, new species.

(Figures 1–3, 5, 6.)

Diagnosis. Suboval *Platyodon*, with anteriorly inflated valves, prominent, strongly incurved, subcentral beaks, short anterior dorsal margin, gently rounded ventral margin and weak concentric ribs.

Description. Shell small to medium-sized, fairly thick, with suboval-trigonal outline, inequilateral, equivalve, slightly longer than high; beaks prominently elevated, strongly incurved, slightly opisthogyrate; valves strongly inflated in anterior region, less so posteriorly; left valve more convex than right valve; anterior dorsal margin short, straight, slopes from umbo to anterior edge at angle of about 45°; anterior margin broadly rounded; posterior dorsal margin slightly longer than anterior dorsal margin, gently concave; extreme posterior edge subacutely truncated; with narrow, lenticular siphonal gape; anterior dorsal and posterior dorsal margins form angle of about 90° at umbo; ventral margin subevenly and broadly rounded; valves ornamented by numerous, (poorly preserved) broad, wavy concentric lamellae with narrow interspaces; no distinct radial striae visible.

Dimensions.

UCMP no.	Length (mm.)	Height (mm.)	Maximum diameter (mm.)
15471	25.2	22.1	17.4
15472	43.0	39.9	32.1
15473	41.2	32.2	28.3
15474	38.0	26.0	24.9
15922	-	30.5	28.0
15923 (incomplete)	31.7	32.8	29.6
15925 (incomplete)	30.4	29.5	24.4

Holotype. UCMP no. 15471, locality A-7762.

Paratypes. UCMP nos. 15472–15474, 15922, 15923, 15925, from the type locality.

Occurrence. From basal San Ramon formation, locality A-7762 along Industrial Highway, Contra Costa County, California.

Age. Middle Oligocene.

Remarks. *Platyodon pecki* Adegoke, new species, is characterized by its rather small size, subovate-trigonal outline, and narrow lenticular siphonal gape.

The oval, nonquadrately elongate outline, narrow siphonal gape, less prominently elevated umbonal-ventral ridge distinguish this species from other Cenozoic species of *Platyodon* such as *P. piedraensis* Wiedey, *P. nipponica* Uozumi and Fujie, *P. clarki* Adegoke, new species, and the Recent species *P. cancellatus* (Conrad). These latter species have a more or less subquadrate outline, more robust and strongly inflated valves. They are more abruptly truncated posteriorly, have wider siphonal gapes, and stronger concentric ribs than the new species.

Platyodon pecki Adegoke, new species, is named in honor of Mr. J. H. Peck, Jr., of the Museum of Paleontology, University of California, Berkeley.

Platyodon piedraensis Wiedey.

Platyodon piedraensis Wiedey, 1929, Jour. Paleo., vol. 3, p. 289, pl. 33, fig. 2. Loel and Corey, 1932, Univ. Calif. Publ., Bull. Dept. Geol. Sci., vol. 22, p. 233, pl. 45, fig. 7.

Diagnosis. A very large species of *Platyodon* with heavy subcentral beaks, short, subequal anterior and posterior dorsal margins, abruptly truncated posterior margin with wide, oval to subcircular siphonal gape.

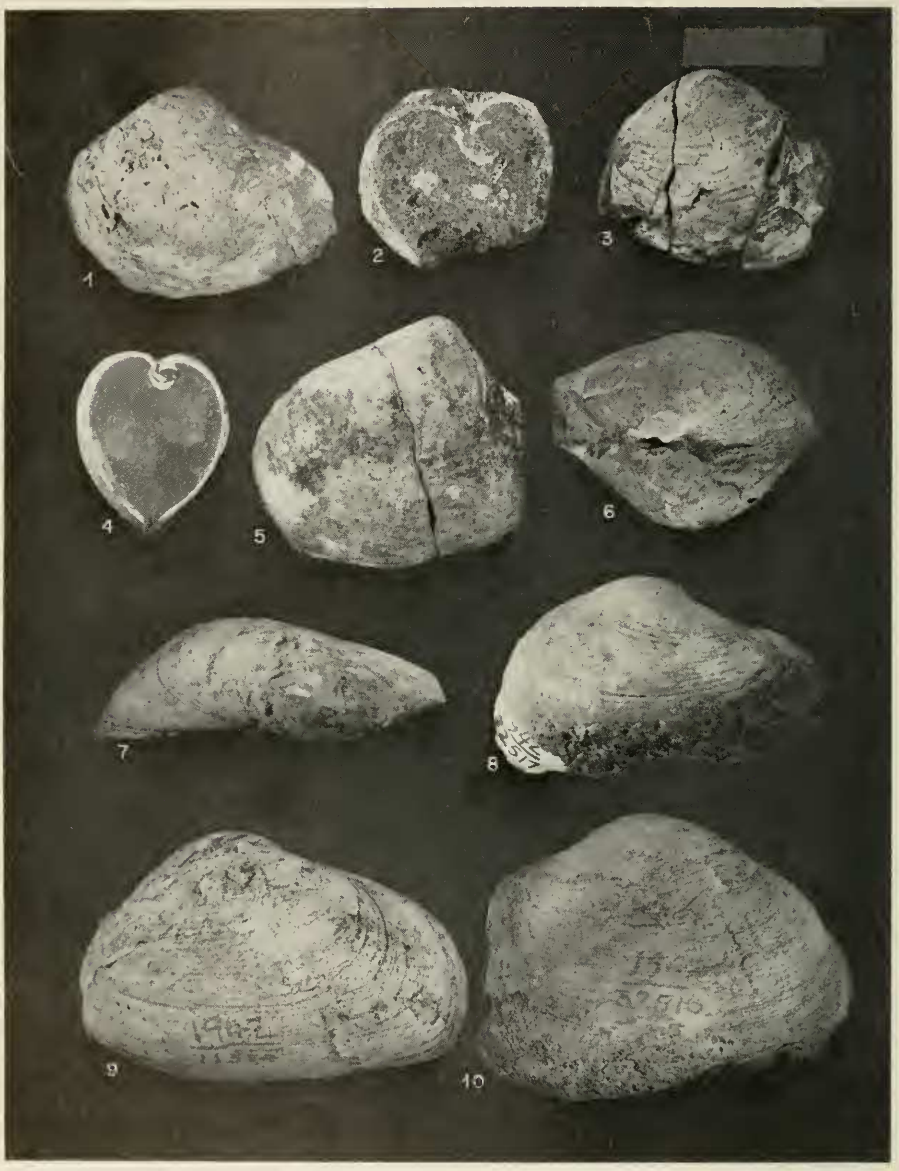
Original description. "Shell of moderate size, equivalve, inequilateral, very highly gibbose, nearly as thick (combined valves) as long; hinge area not long; anterior end of shell abruptly truncated and very widely gaping; basal margin not long, gently rounded; posterior extremity lacking in type; umbones high, broad, and pointed indistinctly forward; posterior dorsal areas in combined valves form a flattened area; sculpture consists of very numerous, more or less evenly spaced, concentric laminae or ridgelets. Height, 58 mm.; breadth, 63+ (20?) (the probable length of part broken away) mm.; thickness, combined valves, 58 mm."

Holotype. Leland Stanford Junior University type collection, type no. 521, from LSJU locality 441.

Occurrence. *Platyodon piedraensis* was collected from the head of Corral de Piedra Creek, about 5 miles east of San Luis Obispo, California (Wiedey, 1929; Loel and Corey, 1932).

Range. Early Miocene, Vaqueros formation.

Remarks. This species is closely similar to the Recent *P. cancellatus* (Conrad) and to *P. nipponica* Uozumi and Fujie. It may be readily distinguished from the former by its shorter anterior and posterior margins, its heavier thicker shell with more numerous concentric ribs and the absence of radial striae. From *P. nipponica* Uozumi and Fujie, it may be distin-



Figures 1–3, 5, 6. *Platyodon pecki* Adegoke, new species.
Figures 1, 6. Paratype, Univ. Calif. Mus. Paleo. no. 15473, ×0.9, locality A-7762, San Ramon formation. Figure 2. Paratype, UCMP no. 15922, ×0.8, locality A-7762, San Ramon forma-

guished by its slightly more elongate valves and finer, subequal ribs. *P. nipponica* has a more trigonal outline and irregular coarse ribs. Comparison of these two species suggests very close relationship. They seem to be more closely related to one another than either of them is to *P. cancellatus*.

Platyodon clarki Adegoke, new species.

(Figures 7–10, 18.)

Mya (*Platyodon*) *cancellatus* Conrad. Clark, 1915, Univ. Calif. Publ., Bull. Dept. Geol., vol. 8, p. 419, pl. 64, fig. 1. Nomland, 1917, Univ. Calif. Publ., Bull. Dept. Geol., vol. 10, p. 300; not Conrad, 1837.

Mya (*Platyodon*) *cancellata* Conrad. Grant and Gale, 1931, San Diego Soc. Nat. Hist., Mem., vol. 1, pp. 415, 416 (in part); not Conrad, 1837.

Diagnosis. Thick-shelled *Platyodon* with triangular-subquadrate outline, prominently raised umbonal-ventral ridge, posteriorly located beaks, elongate anterior margin, and short, truncated posterior margin.

Description. Shell medium to large-sized, length varying from about 27.0 mm. to 85.0 mm., and height varying from about 18.0 mm. to 67.0 mm.; equivalve, strongly inequilateral, with subovate to subquadrate outline; beaks narrow, prominently elevated, slightly prosogyrous; with conspicuously elevated ridge running from umbo to anterior third of ventral margin; umbonal ridge subequally developed in both valves; anterior dorsal margin elongate, slopes from umbo at angle of about 25 degrees, merges insensibly into broadly rounded extreme anterior margin; a shallow depression runs from anterior edge of umbo separating umbonal ridge from anterior slope of shell; posterior dorsal margin short, about one-third the length of anterior dorsal margin, slopes abruptly from umbo at an angle of about 45 degrees, extreme posterior margin abruptly truncated producing subquadrate outline, and rather wide, suboval siphonal gape; ventral margin straight or slightly convex, makes sharp junction of about 120 degrees with anterior margin around distal rim of umbonal ridge; sculpture consists of numerous, subequal, evenly spaced, concentric laminae, and weakly developed radial striae; ribs coarser and fewer near umbones, more numerous, and more closely packed near ventral margin; ribs more pronounced on umbonal ridge and on anterior slope, less prominent in posterior part of valve.

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tion. Figure 3. Holotype, UCMP no. 15471, ×1.2, locality A-7762, San Ramon formation. Figure 5. Paratype, UCMP no. 15472, ×0.9, locality A-7762, San Ramon formation.

Figure 4. *Platyodon cancellatus* (Conrad), ×0.9. Hypotype, UCMP no. 30109, locality 1694, Recent, Bolinas Bay, California.

Figures 7–10. *Platyodon clarki* Adegoke, new species.

Figures 7, 9. Holotype, UCMP no. 11555, ×0.9, locality 1942, San Pablo group. Figure 8. Paratype, UCMP no. 32517, ×0.9, locality 1942, San Pablo group. Figure 10. Paratype, UCMP no. 32516, ×0.6, locality 1942, San Pablo group.

DIMENSIONS.

UCMP no.	Length (mm.)	Height (mm.)	Maximum diameter (mm.)
11555	58.9	39.9	23.3
32501 (incomplete)	24.0	17.6	11.3
32511 (incomplete)	30.7	23.3	11.1
32513 (incomplete)	41.2	36.0	15.1
32514 (incomplete)	44.5	33.8	16.0
32516	85.0	67.3	35.0
32517	52.0	32.0	17.7
32518	46.4	27.3	14.0
32520	52.4	30.9	17.4

HOLOTYPE. Univ. Calif. Mus. Paleo. no. 11555, locality 1942.

PARATYPES. UCMP nos. 32501, 32511, 32513–32514, 32516–32518, and 32520, all from type locality.

OCCURRENCE. Locality 1942, San Pablo group.

RANGE. Late Miocene.

REMARKS. *Platyodon clarki,* new species, is characterized by its prominently elevated umbonal ridge, wide posterior gape and the posteriorly located beak. It is very similar to the Recent *P. cancellatus* (Conrad) from which it may be readily distinguished by its thicker shell, smaller length to height ratio, more abruptly truncated posterior margin, posteriorly located beaks, rather oval outline, and wider gape. *Platyodon cancellatus* is more elongate and has a more quadrate outline than the new species.

Platyodon clarki, new species, is slightly more elongate, less trigonal, and more unevenly convex than *P. nipponica* Uozumi and Fujie. Additionally, its ribs are finer, more numerous, subequal, and more evenly spaced than the coarse, irregular ribs of the Japanese Miocene species.

From *P. piedraensis* Wiedey, the new species may be distinguished by its less bulky shape, narrower, more incurved, posteriorly located beaks, narrower posterior gape, and more prominently elevated umbonal ridge.

One single extra-large specimen of *P. clarki,* new species (paratype no. 32516, fig. 10) was collected from the type locality. Apart from the extremely large size and wider posterior gape, its characters are similar to those of other normal-sized individuals.

Platyodon clarki, new species, is named in honor of B. L. Clark who first reported this species from the San Pablo group.

Platyodon colobus Woodring.

Platyodon colobus WOODRING *in* Woodring, Stewart and Richards, 1941. U. S. Geol. Survey, Prof. Paper 195, p. 95, pl. 21, figs. 1, 2.

DIAGNOSIS. *Platyodon* with trigonal outline, well inflated valves, convex anterior dorsal and concave posterior dorsal margins; anterior dorsal margin slightly longer than posterior dorsal margin; beaks located posteriorly and opisthogyrate; valves ornamented by prominent concentric and radial ribs.

Range. Late Pliocene. Four specimens were collected at the base of the "*Neverita* zone" of the San Joaquin formation (Woodring *et al.*, 1941, p. 95).

Remarks. According to Woodring (*in* Woodring *et al., loc. cit.*), this species is related to the Miocene *P. piedraensis* Wiedey from which it differs by its shorter valves, narrower siphonal gape and its radial sculpture. From *P. cancellatus* (Conrad), the species may be distinguished by its much shorter and higher, trigonal valves.

The short trigonal shape of *P. colobus* closely resembles that of *P. pecki* Adegoke, new species, but may be distinguished from the latter by its more convex valves. more posterior beaks, and its prominent radial laminae.

Platyodon cancellatus (Conrad).

(Figures 4, 15, 19.)

Mya (*Platyodon*) *cancellata* Conrad, 1837, Jour. Acad. Nat. Sci. Phila., vol. 7, p. 236, pl. 18, fig. 2. Packard, 1918, Univ. Calif. Publ. Zool., vol. 14, p. 285, pl. 29, figs. 2 a, b. Grant and Gale, 1931, San Diego Soc. Nat. Hist., Mem., vol. 1, pp. 415, 416 (in part), pl. 24, figs. 3 a, b.

Platyodon cancellatus Conrad. Carpenter, 1864, British Assoc. Adv. Sci., Rept. for 1863, p. 637. Arnold, 1903, Calif. Acad. Sci., Mem., vol. 3, p. 179.

Platyodon cancellatus (Conrad). Yonge, 1951, Univ. Calif. Publ. Zool., vol. 55, pp. 401–408, figs. 1–3; 1951a, Research, vol. 4, p. 164, fig 1E.

Not *Mya* (*Platyodon*) *cancellatus* Conrad. Clark, 1915, Univ. Calif. Publ., Bull. Dept. Geol., vol. 8, p. 419, pl. 64, fig. 1 (= *P. clarki* Adegoke, new species); not Nomland, 1917, Univ. Calif. Publ., Bull. Dept. Geol., vol. 10, p. 300.

Diagnosis. A medium-sized species of *Platyodon* with rounded elongate anterior, elongate and truncated posterior, numerous prominent lamelliform growth lines, and fainter, irregular radial striae.

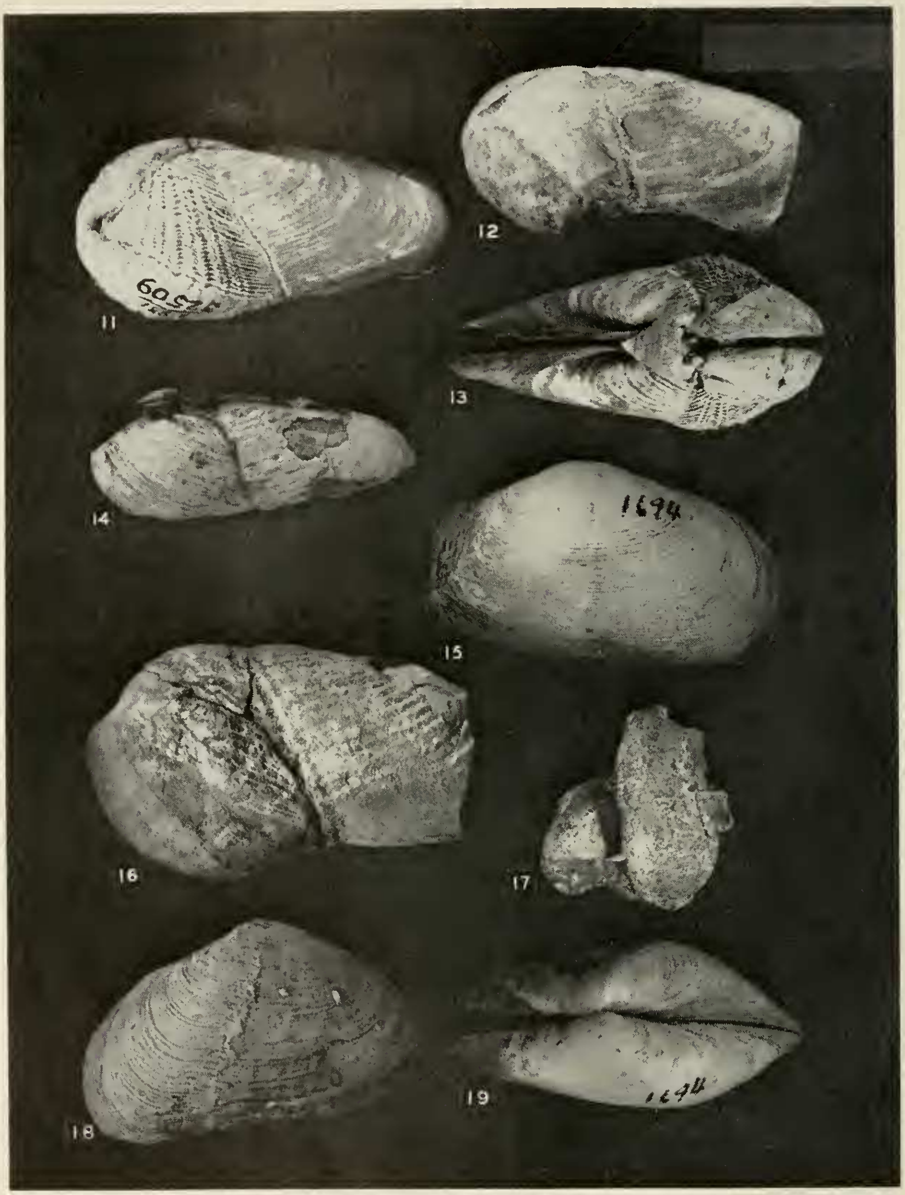
Hypotypes. UCMP nos. 15926 and 30109, locality 1694.

Range. Late Pliocene to Recent. This species was recorded from the Pleistocene upper San Pedro series of southern California. It is found today from Bolinas Bay, middle California, to San Diego (according to Grant and Gale, 1931).

Suborder PHOLADINA
Superfamily PHOLADACEA
Family PHOLADIDAE
Genus **Penitella** Valenciennes

Penitella Valenciennes, 1846, *in* Abel du Petit-Thouars, Voyage Autour du Monde sur la Frégate La Vénus, Atlas de Zoologie, Mollusques, pl. 24.

Type species: (subsequent designation, Habe, 1952),
Penitella conradi Valenciennes.



FIGURES 11, 13. *Penitella penita* (Conrad), ×1.1. Hypotype, Univ. Calif. Mus. Paleo. no. 32509, locality B-831, Recent, Ocean Beach, California.

FIGURES 12, 16–17. *Penitella durhami* Adegoke, new species.

FIGURE 12. Paratype, UCMP no. 30102, ×1.1, locality A-7762, San Ramon formation. FIGURE 16. Holotype, UCMP no. 30101, ×0.9, locality A-7762, San Ramon formation. FIGURE 17. Paratype, UCMP no. 32506, ×0.9, sand-pipes, locality A-7762, San Ramon formation.

Penitella lorenzana (Clark).

(Figures 14, 27.)

Pholadidea (*Penitella*) *lorenzana* Clark, 1924, Univ. Calif. Publ., Bull. Dept. Geol. Sci., vol. 15, p. 107, pl. 18, figs. 5, 6.

Not *Pholadidea* (*Penitella*) *lorenzana* Clark. Weaver, 1953, Univ. Wash. Publ. Geol., vol. 7, p. 60 (=*Penitella durhami* Adegoke, new species).

Diagnosis. *Penitella* with elongate, slender shell, subequal anterior and posterior diameters, lacking posterior truncation as well as anterior and posterior gapes, siphonal gap filled by callus plate, entire surface ornamented by simple, wavy, concentric, weakly spinose lamellae.

Original description. "Shell elongate subovate; beaks in anterior third of shell, each covered by a callus which stands out very prominently on anterior dorsal edge. Anterior portion of shell separated from posterior portion by a fairly deep tranverse furrow, between beaks and above the middle of ventral edge. Anterior end bluntly pointed. On specimens at hand siphonal gap is filled by a callus plate; posterior end subacutely rounded, not gapping, as on shells belonging to the Recent species, *P. penita* Conrad. Surface of shell anterior to tranverse furrow covered by concentric spinose wavy lamellae; the spines on the different lamellae are in line, and so give the effect of a number of fairly distinct radiating lines crossing the wavy lamellae. Surface of shell posterior to tranverse lamellae smooth, except for somewhat irregular, fairly heavy incremental lines; a rather narrow, elongate quadrate metaplax with upper surface rather strongly concave, hinge plate not exposed. Dimensions: length 37 mm.; height 15 mm."

Holotype. Univ. Calif. Mus. Paleo. no. 30323, locality 1131.

Paratype. UCMP no. 33491, from type locality.

Occurrence. UCMP locality 1131, San Ramon formation, southwest of Walnut Creek, California.

Range. Middle Oligocene. This species has been recorded only from the type locality. Specimens from the basal San Ramon sandstone of the East limb of the Pacheco syncline (locality A-7762) referred to this species by Weaver (1953, p. 60) differs significantly from Clark's species (see below), and are here described as *Penitella durhami,* new species.

At the type locality, *P. lorenzana* is associated with the following mollusks: *Acila muta* Clark, *Anomia inconspicua* Clark, *Antigona mathewsonii* (Gabb), *Anadara (Anadara) mediaimpressa* (Clark), *Glycymeris tenuimbricata* Clark,

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Figure 14. *Penitella lorenzana* (Clark), ×1.2. Holotype, UCMP no. 30323, locality 1131, San Ramon formation.

Figures 15, 19. *Platyodon cancellatus* (Conrad), ×0.9. Hypotype, UCMP no. 15926, locality 1694, Recent, Bolinas Bay, California.

Figure 18. *Platyodon clarki* Adegoke, new species, ×1. Paratype, UCMP no. 32520, locality 1942, San Pablo group.

Mytilus mathewsonii Gabb, *Yoldia cooperii supramontereyensis* Arnold, *Bruclarkia gravida* Gabb, and *Molopophorus biplicatus* (Gabb). Many of these are generally regarded as indicative of the Oligocene epoch (Clark, 1924, p. 107; 1929, p. 17; Arnold, 1906, pp. 15–17).

Remarks. *Penitella lorenzana* (Clark) belongs to the same general group as the Recent West American *P. penita* (Conrad). It may be distinguished from the latter by its elongate, spindle shape. It is longer in proportion to height, and the anterior region is much less inflated than in the latter. The attenuated extreme posterior end and absence of a posterior gape in *P. lorenzana* are characteristic and distinguish it from *P. penita* with its characteristically truncated posterior end with a relatively wide oval gape. Both the transverse furrow and the callum are relatively less strongly developed in *P. lorenzana* than in *P. penita.*

The exterior ornamentation in *P. lorenzana* is relatively very simple. It consists of about 20–25 simple, wavy, spinose concentric lamellae. Spines are rather weakly developed and do not form conspicuous radial ridges as in *P. penita*. Sand-filled burrows of this species are unknown.

Penitella durhami Adegoke, new species.

(Figures 12, 16, 17, 20–26, 28.)

Pholadidea (*Penitella*) *lorenzana* Clark. Weaver, 1953, Univ. Wash. Publ. Geol., vol. 7, p. 61; not Clark, 1924.

Diagnosis. *Penitella* with elongate, well inflated valves; robust, rounded anterior; slenderer, less rounded, truncated posterior; with prominently depressed umbonal-ventral sulcus; flanked by two narrow but prominent rounded ridges; convex dorsal margin, and markedly concave ventral margin.

Description. Shell small to large, with elongate oval outline; immature specimens gaping wide anteriorly and posteriorly; umbonal-ventral sulcus conspicuously depressed, flanked by two narrow but prominently elevated ridges which are further delineated from rest of shell by shallow broad depressions (see fig. 28); umbonal-ventral sulcus divides valves into two distinct and very unequal parts; anterior portion small, about half length of posterior portion, remarkably robust, inflated, and rounded, with subcircular cross-sectional outline; sharp ventral concave flexure coincides with ventral portion of umbonal-ventral sulcus, further delimiting rounded anterior from the less high, laterally compressed posterior; protoplax strongly developed, separated from beak and callum by narrow, depressed umbonal reflection; callum well developed, protrudes beyond beaks, closes pedal gape in adults; anterior slope ornamented by numerous wavy concentric ridges with poorly defined, radially arranged spines; posterior region of shell longer than anterior region, flattened laterally, not as high as anterior region; posterior dorsal margin prominently ridged, and convex; posterior ventral margin keeled, markedly concave; posterior slope and disc ornamented by wide concentric ribs with narrow interspaces; posterior extremity sharply truncated, with wide subcircular siphonal gape.

Dimensions.

UCMP no.	Length (mm.)	Maximum height (mm.)	Maximum diameter (mm.)
30101	58.9	34.9	32.8
30102	41.6	20.1	19.5
30103	18.8	9.0	11.3
30104	39.5	24.0	27.6
30105	32.4	22.9	21.3
30108	35.8	19.6	22.9
32493	39.0	22.4	23.0
32494 (incomplete)	28.9	18.2	17.7
32495 (incomplete)	31.7	21.4	23.2
32496	35.9	21.4	22.0
32497 (incomplete)	27.6+	14.3	13.1

Holotype. UCMP no. 30101, locality A-7762.

Paratypes. UCMP nos. 30102–30105, 30108, 32493–32497, 32503–32508, locality A-7762.

Occurrence. Basal San Ramon formation, locality A-7762, along Arnold Industrial Highway, Contra Costa County, California.

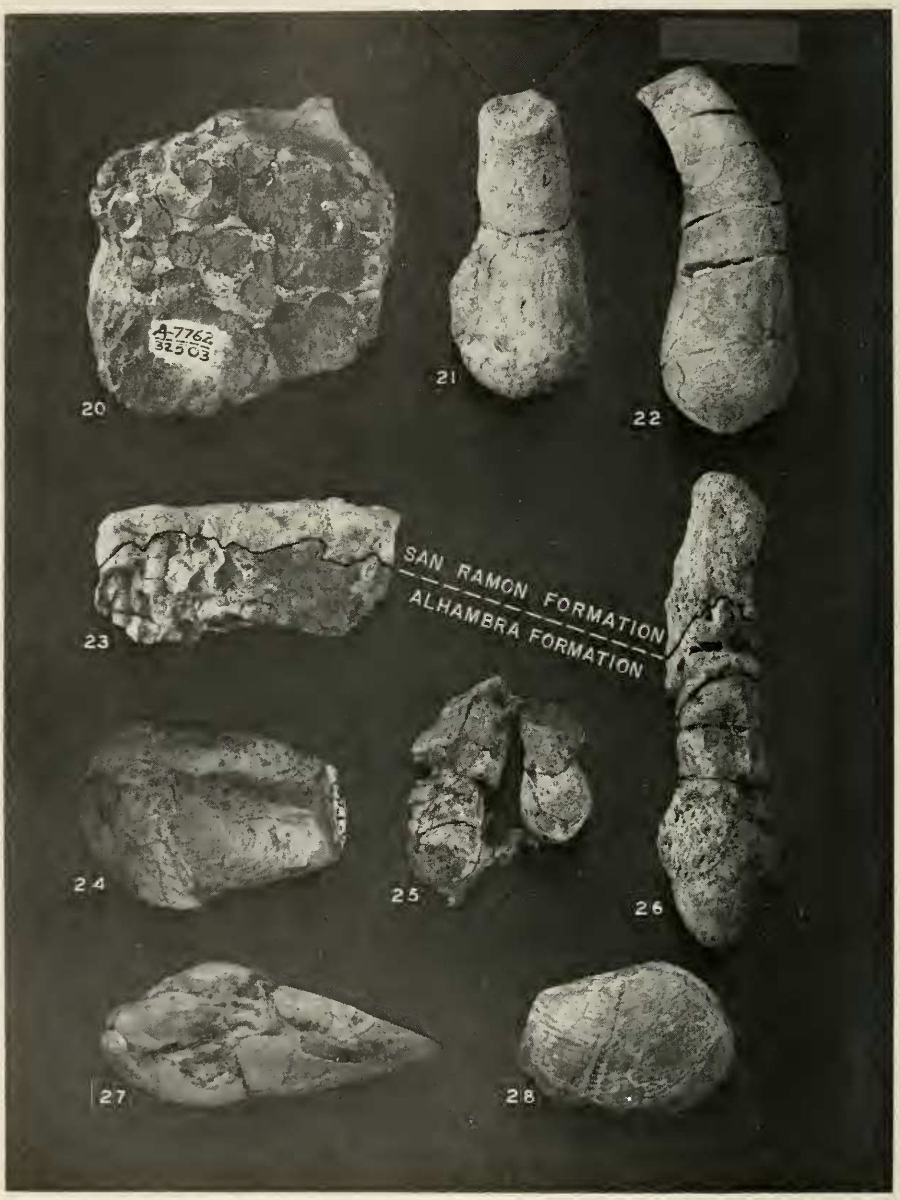
Range. Middle Oligocene.

Remarks. *Penitella durhami* Adegoke, new species, is characterized by its robust, rounded anterior region. Its well developed callum and protoplax show that it is related to the Recent *P. penita* (Conrad) from which it differs by its less deeply impressed umbonal-ventral sulcus, less prominent protoplax, weaker anterior concentric lamellae with weaker spines and faintly developed radial ridges. The lamellae in *P. penita* are strongly elevated and flexed and bear many prominently elevated, radially arranged spines. The posterior concentric ornamentations of the new species are slightly more numerous, coarser and more distantly spaced than in *P. penita*.

From *P. lorenzana* (Clark), the new species may be distinguished by its heavier, robust, and more bulky valves, the rounded anterior region, and the truncated posterior. The entire ventral margin of the new species is markedly concave whereas the same margin is gently convex in *P. lorenzana*.

Penitella durhami, new species, may be distinguished from *P. kotakae* (Kanno and Matsuno) from the Japanese Tertiary by its more elongate valves with greater length to height ratio. It may be further distinguished by the more rounded anterior region, abruptly truncated posterior, and the simpler ornamentation.

Several sand-pipes belonging to *P. durhami,* new species, were collected by



Figures 20, 23. Hand specimens showing *a*. sand-pipes created by *Penitella durhami* Adegoke, new species, *b*. closely packed nature of sand-pipes, *c*. the disconformable relationship between the Eocene Alhambra formation and the overlying San Ramon formation. Paratype, UCMP no. 32505, ×0.6, locality A-7762, Alhambra and San Ramon formations.

Figures 21, 22, 25, 26. Sand-pipes created by *Penitella durhami* Adegoke, new species, ×0.6, locality A-7762. Figure 21. Paratype, UCMP no. 32508. Figure 22. Paratype, UCMP the writer from the type locality. Some of these are illustrated (see figs. 11–28). The tubes have subcircular outlines and the occupants fit tightly into the burrows. The burrows are commonly straight. A few curved ones were, however, collected (figs. 22, 26).

The new species is named in honor of Professor J. Wyatt Durham who collected the specimens and drew my attention to them.

Penitella fitchi Turner.

Penitella fitchi Turner, 1955, Johnsonia, vol. 3, no. 34, pp. 71–75, pls. 40–42.

Diagnosis. *Penitella* with thin closely appressed umbonal reflections, incompletely developed callum in adult stage, siphonoplax composed of numerous, chitinous, leaf-like layers, mesoplax broadly rounded to truncate posteriorly, rounded anteriorly and lacking lateral wings.

Range. Recent. Known only from type locality, Bahía San Bartolomé, Baja California.

Remarks. According to Turner (1955), *P. fitchi* does not appear to be closely related to any other species in the genus. It appears more closely related to *P. conradi* than to other penitellas. Its partially developed callum and the numerous, thin, chitinous laminae composing its siphonoplax distinguish it from *P. conradi*. *Penitella fitchi* approaches *P. penita* in size and both are found living together. They differ in form of mesoplax and siphonoplax and in the complete callum of the latter.

Penitella conradi Valenciennes.

Penitella conradi Valenciennes, 1846, *in* Abel du Petit-Thouars, Voyage Autour du Monde sur la Frégate La Vénus, Atlas de Zoologie, Mollusques, pl. 24, fig. 1. Turner, 1955, Johnsonia, vol. 3, no. 34, pp. 75–80.

Diagnosis. *Penitella* usually found boring into *Haliotis* or other shells; occasionally in clay or soft stone. Umbonal reflections broad and closely appressed for their entire length. Mesoplax truncate posteriorly, pointed anteriorly, lacking lateral wings. Siphonoplax heavy.

Range. Recent.

←

no. 32507, showing a curved sand-pipe. Note anterior end of mollusks visible in distal swollen portion of these sand-pipes. Figure 25. Paratype, UCMP no. 32504. Specimen shows two sand-pipes side by side. Anterior ends of mollusks visible at swollen ends. Figure 26. Paratype, UCMP no. 32505, specimen showing origin of sand-pipe in San Ramon formation and its continuation into underlying Alhambra formation.

Figures 24, 28. *Penitella durhami* Adegoke, new species, ×0.9, locality A-7762, San Ramon formation. Figure 24. Paratype, UCMP no. 30104; Figure 28. Paratype, UCMP no. 30105.

Figure 27. *Penitella lorenzana* (Clark), ×1.2. Paratype, UCMP no. 33491, locality 1131, San Ramon formation.

Table 1. *Temporal distribution of species of* Platyodon *Conrad in the eastern and northwestern Pacific.*

LIST OF SPECIES	PALEOCENE	EOCENE	OLIGOCENE	MIOCENE	PLIOCENE	PLEISTOCENE	RECENT	
Platyodon cancellatus (Conrad)					—?— —?—	■	■	EASTERN PACIFIC
Platyodon colobus Woodring					■			
Platyodon clarki, new species				■				
Platyodon piedraensis Wiedey				■				
Platyodon pecki, new species			■					
Platyodon nipponica Uozumi and Fujie				■				NORTHWESTERN PACIFIC

Remarks. The heavier, less diverging siphonoplax with pronounced white, granular, calcareous lining distinguish *Penitella conradi* from *P. penita* (Conrad). It may be separated from *P. gabbi* (Tryon) by its very closely appressed umbonal reflection, and possession of a siphonoplax.

Penitella gabbi (Tryon).

Zirphaea gabbi Tryon, 1863, Proc. Acad. Nat. Sci. Phila., p. 10, pl. 1, fig. 1.

Pholas (*Zirfaea*) *gabbi* (Tryon). Grant and Gale, 1931, San Diego Soc. Nat. Hist., Mem., vol. 1, pp. 432, 433, pl. 24, fig. 2.

Zirfaea gabbi (Tryon) var., Stewart *in* Woodring *et al.*, 1941, U. S. Geol. Surv., Prof. Paper 195, p. 96, pl. 34, fig. 7.

Penitella gabbi Tryon. Turner, 1955, Johnsonia, vol. 3, no. 34, pp. 85–88, pls. 52–54.

Diagnosis. *Penitella* in which callum does not protrude beyond beaks, umbonal reflections narrow, lightly appressed over umbos and free anteriorly. Adult mesoplax rounded posteriorly, pointed anteriorly, and with broad lateral wings. Siphonoplax lacking; siphons pustulose.

Range. Pliocene to Recent.

Remarks. *Penitella gabbi* differs from *P. penita* to which it is most closely related by lacking the siphonoplax; more narrowly rounded posterior margin; shorter, broader mesoplax; lighter, thinner periostracum. Besides, the umbonal reflections of the former are narrow, free anteriorly and lightly appressed over the umbos.

A small variety of *P. gabbi* from the late Pliocene, San Joaquin formation ("*Pecten coalingaënsis* zone") of the Coalinga region was described as *Zirfaea gabbi* (Tryon) *femii* Adegoke by the writer (Adegoke, in press). The minute size of this subspecies is characteristic; the dimensions of the holotype being: length 30.4 mm., height 16.2 mm., thickness of both valves 15.5 mm.

Penitella penita (Conrad).

(Figures 11, 13.)

Pholas penita Conrad, 1837, Jour. Acad. Nat. Sci. Phila., vol. 7, p. 237, pl. 18, fig. 7.

Penitella penita Conrad. Tryon, 1862, Proc. Acad. Nat. Sci. Phila., vol. 14, p. 215. Gabb, 1869, Geol. Surv. Calif., Palaeo., vol. 2, p. 88. Turner, 1955, Johnsonia, vol. 3, no. 34, pp. 80–85, pls. 5, 47–51.

Pholadidea penita Conrad. Carpenter, 1864, British Assoc. Adv. Sci., Rept. for 1863, p. 525. Dall, 1909, U. S. Geol. Survey Prof. Paper 59, p. 134. Packard, 1918, Univ. Calif. Publ. Zool., vol. 14, p. 288, pl. 30, figs. 3 a, b.

Pholadidea (Penitella) penita Conrad. Arnold, 1903, Calif. Acad. Sci., Mem., vol. 3, p. 184.

Pholadidea (Pholadidea) penita (Conrad). Grant and Gale, 1931, San Diego Soc. Nat. Hist., Mem., vol. 1, p. 434, pl. 24, figs. 1 a, b.

Diagnosis. *Penitella* with callum protruding beyond beaks, umbonal reflections broad, thin and very closely appressed their entire length; mesoplax sharply pointed posteriorly, truncate anteriorly, and having short, pointed lateral wings; siphonoplax composed of two heavy, flexible, chitinous flaps which are often diverging; siphons smooth.

Hypotype. Univ. Calif. Mus. Paleo. no. 32509, locality B-831.

Occurrence. This species has been reported from the Pliocene Empire formation, Coos Bay, Oregon (Dall, 1909); the Pliocene of Santa Barbara (Gabb, 1869); and the Pleistocene San Pedro series (Arnold, 1903). Its present range is from "Bering Island, Siberia south at least as far as Bahía San Bartolomé, Baja California" (Turner, 1955).

Range. Pliocene to Recent.

Remarks. The diagnostic characters of this species and the differences between it and other Recent and fossil penitellas were discussed in detail by Turner (1955) and in the discussion of other species (above). Its flexible, leathery siphonoplax, the characteristic mesoplax (see diagnosis above), and smooth siphons clearly distinguish *P. penita* from other described penitellas.

Evolutionary and Biogeographic Considerations

Present known records of species of *Platyodon* and *Penitella* on both the American and Asiatic sides of the Pacific (see tables 1 and 2) as well as in the western Atlantic (see Turner, 1954; 1955) are too scanty to permit one to make an accurate and intelligible interpretation of evolutionary trends and relationships or to suggest possible trans-Pacific and Pacific-Atlantic migratory

TABLE 2. *Temporal distribution of species of* Penitella *Valenciennes in the eastern and northwestern Pacific.*

LIST OF SPECIES	PALEOCENE	EOCENE	OLIGOCENE	MIOCENE	PLIOCENE	PLEISTOCENE	RECENT	
Penitella fitchi Turner							■	EASTERN PACIFIC
Penitella conradi Valenciennes							■	
Penitella gabbi (Tryon)					■	■	■	
Penitella penita (Conrad)					■	■	■	
Penitella durhami, new species			■					
Penitella lorenzana Clark			■					
Penitella chishimana (Habe)							■	NORTHWESTERN PACIFIC
Penitella kamakurensis (Yokoyama)							■	
Penitella katakae (Kanno and Matsuno)				■				

and dispersal routes and the times they occurred. No attempt has so far been made at a synthesis of western Atlantic and northwestern Pacific fossil and Recent occurrences.

The results presented in this paper (summarized in tables 1 and 2) indicate that a continuous evolutionary succession of species of both genera can be demonstrated in the northeastern Pacific between the middle Oligocene and Recent, whereas Japanese and other northwestern Pacific records are few and sporadic (tables 1 and 2). This would indicate that species of both genera had their origin and evolutionary history in the eastern Pacific and were dispersed from here into Atlantic and northwestern Pacific waters. *Penitella kotakae* (Kanno and Matsuno) from the Japanese middle to late Miocene strata closely resembles and was probably derived from one of the Middle Oligocene taxa from California. The morphologic characters of the former favor derivation from a form such as *Penitella durhami*, new species.

The close relationship between *Platyodon piedraensis* Wiedey from the California lower Miocene, Vaqueros formation and *P. nipponica* Uozumi and Fujie from the middle Miocene to late Miocene Chikubetsu formation of Japan was emphasized earlier. This would suggest that the Japanese stock was established by migrants from the northeastern Pacific.

A consideration of the geographic and temporal distribution of present known species of *Platyodon* and *Penitella* indicate that trans-Pacific migrations from the American to the Asiatic side may have occurred some time between the early and middle Miocene. This migratory direction is contrary to the commonly encountered pattern in which most species are known to have migrated from the Asiatic side of the Pacific to the American side (see MacNeil, 1965).

REMARKS

The peculiar association of *Platyodon pecki,* new species, and *Penitella durhami,* new species, in the basal San Ramon formation of Contra Costa County, California deserves some comments. This association is very similar to that observed in the Japanese Miocene Chikubetsu formation by Uozumi and Fujie (1956), who described two types of sand-pipes from that formation. These are: the I-form occupied by *Platyodon nipponica* Uozumi and Fujie, and the II-form which contained shell remains of *Pholadidea* (*Penitella*) *kamakurensis* (Yokoyama) (= *P. kotakae* Kanno and Matsuno).

In this study, only sand-pipes of the II-form were collected. These generally have an elongate, rounded neck, and a relatively shorter, swollen, rounded base. They all contained shell remains of *Penitella durhami,* new species in their swollen distal portions (see figs. 22, 25, 26). It appeared as if the specimens were all buried *in situ.*

The mode of boring of *Platyodon* and *Penitella* has been described by many workers and has recently been reviewed by C. M. Yonge (1951a) and Turner (1954, 1955). It is now generally accepted that both *Platyodon* and *Penitella* bore mechanically into sediments with the aid of their valves (Yonge, 1951, pp. 404–406; 1951a, pp. 163, 164; Uozumi and Fujie, 1956, pp. 364, 368; Turner, 1954, p. 8, also pl. 5). *Platyodon* bores into very soft mudstone (Yonge, 1951, p. 401; Uozumi and Fujie, 1956, p. 367; Kofoid and Miller, 1923), whereas *Penitella* bores into harder, solidified sediments (Yonge, 1951a, p. 161; Uozumi and Fujie, 1956; Turner, 1954, pp. 2, 6; 1955, p. 2), and even concrete (Kofoid and Miller, 1923).

This inference was well documented by Uozumi and Fujie who observed (1956, p. 361) that sand-pipes of the I-form occupied by *Platyodon* were commonly crossed by *Penitella*-bearing II-form sand-pipes but never the reverse condition. They, thereby concluded that during sedimentation, species of *Platyodon* were the first invaders. These burrowed into the soft, muddy, bottom sediments. Invasion of the same pocket by *Penitella* took place at a much later stage after the sediments had been compacted into hard claystone or shale. A condition similar to that described by Uozumi and Fujie was not conclusively demonstrated in this study because *Platyodon*-bearing sand-pipes were not collected.

Another remarkable feature observed in this and other similar studies of boring bivalves is that several specimens of both species occur side by side, in large numbers in small pockets (see figs. 20, 23, 25). So far, each species has commonly been recorded only from one locality. It is hoped that additional collection will in future demonstrate that these boring pelecypods have a wider geographic range than is known presently.

Locality Descriptions

The locality numbers cited here are those of the Invertebrate Catalogue of the Museum of Paleontology, University of California, Berkeley. All the type specimens are deposited in the Museum.

Locality 1131

San Ramon formation, Concord quadrangle, Contra Costa County, California. "½-mile southwest of town of Walnut Creek, in creek bed, about 100 yards to east of Oakland-Antioch bridge; elevation 150 feet; long. 22°4′8″, lat. 37°53′7″."

Locality 1694

Recent, Bolinas Bay, California. Coll.: H. Hemphill.

Locality 1942

San Pablo group, Concord sheet, Contra Costa County, California. On top of east end of long hill, about ½-mile northwest of Joe Mendoza's house, elevation 350 feet, about 1½ miles east of Walnut Creek.

Locality A-7762

San Ramon formation, Walnut Creek quadrangle, Contra Costa County, California. Fossiliferous beds exposed on the north side of the Arnold Industrial Highway (State Route 4), about ½-mile northeast of the Atchison-Topeka, Santa Fe Railroad tunnel. This locality is west of the turn off to Avon. Fossils occur at the contact of the San Ramon and Alhambra formations. This locality is also listed as UCMP locality A-4296, and is probably the same as Weaver's (1953) locality 1238. Coll.: Univ. Calif. Paleo. 103 Class, 1947; J. Wyatt Durham and J. H. Peck, 1951; Adegoke, 1966.

Locality B-831

Recent, Ocean Beach, California. Coll.: W. K. Emerson, 1939.

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